Journal of Arid Environments (1994) 27: 309–323

Water regime in soils and plants along an aridity gradient in central Baja California, Mexico

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(*Received 4 September 1992, accepted by 5 February 1993*)

The Central Desert of Baja California has pronounced climatic gradients. Water storage in the upper metre of soil and leaf water potentials in *Larrea tridentata*, *Simmondsia chinensis* and *Fouquieria columnaris* were monitored during 28 months at six sites. Estimated annual evapotranspiration was 75–150mm in sandy loams, and 45–60mm in sandy soils. Cumulative recharge accounted for ~ 80% of precipitation in loams, but only 50% in sands. During the study period, increased aridity was expressed as longer periods of drought, but there was no less recharge. Weak to moderate relationships were found between soil water content and predawn leaf water potential.

Keywords: arid soils; climatic gradient; mediterranean–tropical ecotone; Sonoran Desert; water budget; water regime; xerophytes

Introduction

Regional differences in soil water regimes result in differences in growth and limits to distribution of plants. A number of studies have characterized water regimes in one (Shreve, 1934; Winkworth, 1970; Sammis & Gay, 1979; Schlesinger *et al.*, 1987) or several arid habitats under the same macroclimate (Hillel & Tadmor, 1962; Branson *et al.*, 1976). However, little information is available on how soil water regimes differ across climatic gradients in dry regions.

The Central Desert of Baja California, which is located in the central third of the peninsula, is characterized by two marked climatic gradients. Along the Pacific Ocean coast, the climate is oceanic: cool and frequently foggy. Along the Gulf of California coast, the climate is continental: dry and hotter in summer and colder in winter than on the western side (Hastings & Turner, 1965). In addition, there is a gradual southward transition, or ecotone, from the mediterranean (winter rain/summer drought) to tropical (summer rain/winter drought) climatic regimes (Hastings & Turner, 1965; Reyes *et al.*, 1988). This ecotone stretches from coast to coast approximately between the 30th and 27th parallels of latitude. Across the ecotone, annual rainfall amounts are fairly uniform and average 100–150 mm, but the timing of precipitation is highly unpredictable (Hastings & Turner, 1965; Reyes *et al.*, 1988). The responses of organisms to differences in the timing and reliability of moisture across this ecotone is of interest to ecologists. Moreover, the

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ability to estimate seasonal water recharge in the large (>100,000 ha) communal landholdings (ejidos), in which cattle production is an important economic activity, may help to improve the management of grazing.

The aims of this study were (i) to compare soil water regimes on similar soils across an aridity gradient, and (ii) to test whether leaf water potential in indicator shrubs can be used to estimate soil water recharge at different sites.

Materials and methods

The area studied is in the northern portion of the ecotone (Fig. 1). The aridity gradient described in the present work cuts across two of the major subdivisions of the Sonoran Desert recognized within Baja California by Wiggins (1980). The sarcophyllous desert, in which *Agave* and *Ambrosia* predominate and the stem succulents *Fouquieria columnaris*, *Pachycereus pringlei*, and *Pachycormus discolor* are common, occurs over much of the central third of the peninsula and extends from the Pacific coast to the mountain summits. East of the divide lies the microphyllous desert, whose vegetation is dominated by *Larrea tridentata*, together with such spiny shrubs as *Fouquieria splendens*, and *Cercidium microphyllum*. The microphyllous desert here is a band ~30 km wide that extends along the Gulf of California coast as far south as Bahía de Los Angeles. Four study sites (El Progreso, Cataviña, Laguna Chapala and El Crucero, Table 1) were established along the axis of the central mountain range and roughly parallel to the boundary between the two vegetation

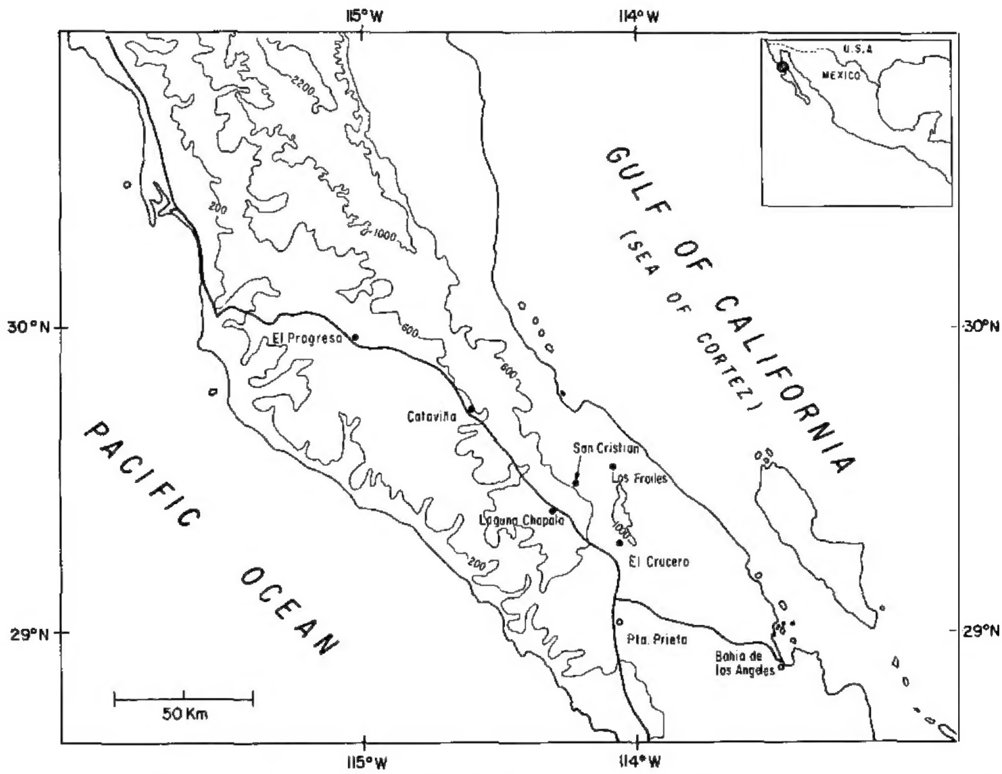

Figure 1. Topographic map of the northern portion of the Central Desert of Baja California showing the location of the study sites (closed symbols) and two other nearby weather stations (open symbols). Altitudes are in metres above sea level.

Table 1. *Description of study sites in the Central Desert of Baja California, Mexico*

Site	Altitude (m)	Perennial plant cover (%)* (dominant species)	Geomorphic position	Slope (%)	Parent material‡	Soil classification	Horizon depth (cm)	Texture‡	pH§	EC‖ (dSm^{-1})
El Progreso	480	16 ± 2·5 ab	Backslope	16	Tuff	Torriorthents	0–27	Loamy sand	7·0	0·6
		(*Ambrosia camphorata*	near wash				27–71	Sandy loam	7·1	1·0
		A. chenopodifolia)					71–135	Sandy loam	7·1	1·4
Cataviña	580	24 ± 3·0 b	Footslope	9	Quartz diorite	Torripsamments	0–58	Sand	6·5	0·6
		(*Larrea tridentata*	with				50–101	Sandy loam	6·8	0·7
		Opuntia molesta)	boulders							
			and tors							
L. Chapala	710	38 ± 6·9 b	Valley	10	Alluvium	Torriorthents	0–33	Loamy sand	7·2	1·3
		(*A. chenopodifolia*	bottom				33–99	Loamy sand	6·7	1·0
		L. tridentata)					99–143	Loamy sand	7·2	1·2
El Crucero	620	28 ± 9·5 b	Midslope on	9	Alluvium	Torripsamments	0–4	Loamy sand	7·4	0·3
		(*Ambrosia dumosa*	dissected				4–25	Sandy loam	7·2	0·2
		L. tridentata)	fan				25–60	Sandy loam	7·4	0·4
							60–70	Sandy loam	7·8	0·3
							70–100	Sandy loam	7·9	0·5
San Cristián	580	27 ± 8·8 b	Footslope	7	Volcanic not	Haplargids	0–43	Loamy sand	7·2	1·5
		(*Agave deserti*	near wash		differentiated		43–81	Silt loam	7·1	13
		Euphorbia misera)					81–>100	Loamy sand	6·5	25
Los Frailes	110	3·5 ± 2·2 a	Valley	3	Quartz diorite	Torripsamments	0–>254	Sand	7·1	0·9
		(*L. tridentata*)	bottom							

* Mean ± standard error of the mean, 25 m transects ($n = 4$), means followed by the same letter are not significantly different ($p \leq 0·05$).
† Gastil *et al.*, 1971.
‡ Soil Survey Staff, 1975.
§ Saturated paste.
‖ Saturation extract.

types. Because of the distances involved, it was impractical to extend the transect southward across the entire ecotone, and instead two additional sites (San Cristián and Los Frailes) were established along an intersecting W–E transect that runs towards the Gulf coast. San Cristián is on the eastern foothills of the central mountains near the boundary between the two phytogeographic provinces, but Los Frailes lies well within the microphyllous desert. Water regimes were characterized in connection with a study of the response of annual plants to the timing of water availability (Walkowiak & Salazar, 1988). In this region, Graham & Franco-Vizcaíno (1992) described soils that developed on the principal geologic substrates, and Franco-Vizcaíno *et al.* (1993) characterized some chemical properties of soils on quartz diorite and basalt parent materials.

Climate

The study sites along the mountain axis were located near long-established weather stations operated by the Ministry of Agriculture and Water Resources (SARH) (Figs 1, 2). A new station was constructed at San Cristián; and a station at Calamajué, on the Gulf coast near Los Frailes, was reactivated. Nevertheless, the study was initiated during a period of

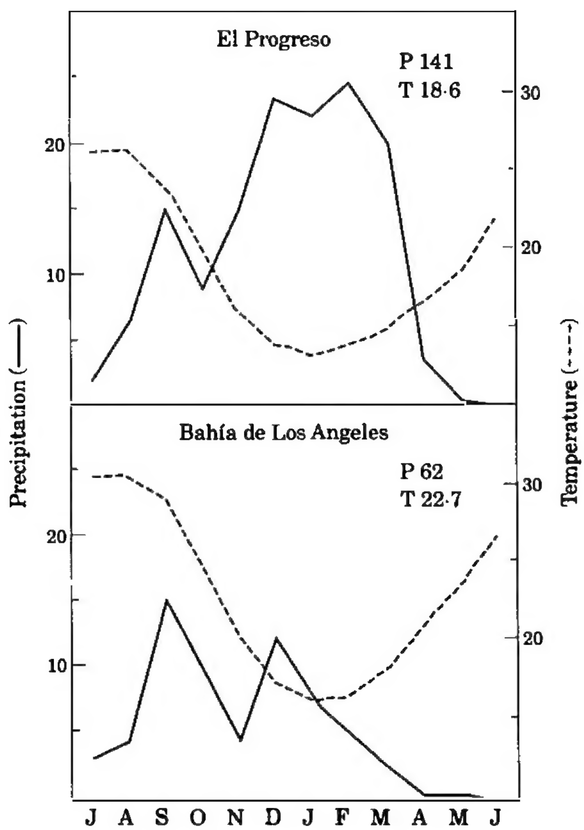

Figure 2. Mean monthly precipitation and temperature for the period 1947–88 at weather stations near the ends of the climatic gradient studied. Mean annual precipitation and temperature are given in the upper right. Source: Ministry of Agriculture and Water Resources (SARH) and Grupo de Meteorología, CICESE.

national budgetary crises which, in addition to the lack of qualified operators, resulted in the loss of most precipitation data for Cataviña, El Crucero (Punta Prieta), San Cristián, and Los Frailes (Calamajué). The data for Laguna Chapala are reliable but incomplete. Complete and reliable records exist only for El Progreso.

Pooled data (1957–86) for the four weather stations along the central highlands show that the average percentage of precipitation that falls during autumn, winter, spring and summer is 37, 42, 3 and 18, respectively. However, at the nearest weather station on the Gulf of California, Bahía de Los Angeles, the percentages are 41, 23, 1 and 35, respectively (unpublished data). In summer, daytime maximum temperatures in the central highlands are frequently >40°C, and in winter minimum temperatures are rarely sub-freezing (Clark *et al.*, 1993). In late fall and winter, frontal storms that originate in the north Pacific generally produce low-intensity precipitation that can persist for two or more days. Summer thunderstorms, associated with the North American monsoon, are usually scattered and rains brief and intense. In autumn, hurricanes can develop widespread precipitation that may last one or more days. In the central highlands, the average percent of precipitation from these tropical storms is 16%, but 40% at Bahía de Los Angeles (unpublished data). Interannual variability in the climate of the Central Desert is strongly influenced by El Niño/Southern Oscillation events (Reyes *et al.*, 1988).

Leaf water potential and soil water content

We sampled plants for leaf water potential and soils for water content at roughly monthly intervals from December 1986 to April 1989. The study area is distant (>300 km) from population centres. Sampling was scheduled on the basis of the availability of vehicles and personnel, and thus occurred more or less randomly in time. Leaf water potential was measured in twigs cut from the woody shrubs creosote bush (*Larrea tridentata* (Sessé & Mac. ex DC.) Coville) and jojoba (*Simmondsia chinensis* (Link) Schneider), and from the stem succulent cirio (boojum tree) (*Fouquieria columnaris* (Kellogg) Hendrickson), by using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Oregon). Predawn and midday readings were made in duplicate on three individuals of each species. Because of the number of measurements, it was necessary after several visits to rotate sampling among different individuals in the community. The chamber's pressure relief valve activated at ~6·5 MPa, and we were frequently unable to measure leaf water potential during the dry months when plant stress is greatest. The loss of these data made establishing the relationship between leaf water potential and soil water content difficult because it is during periods of drought that soil water more clearly exerts control over plant water potential (Branson *et al.*, 1976). At each site, a transect 30–50 m long and some 20 m wide was established in the *Larrea* community. The two other species sampled occurred within that community only at Cataviña and El Crucero. *S. chinensis* occurs along dry water courses adjacent to the transects at El Progreso and San Cristián, and both *S. chinensis* and *F. columnaris* were found on an adjacent hillock at Laguna Chapala. *F. columnaris* does not occur in the transect at San Cristián (although a small, disjunct population was found on a steep hillside ~200 m away), and neither *S. chinensis* nor *F. columnaris* occur at the most extreme (easternmost) site, Los Frailes. Although the sites were selected on the similarity of their plant communities and physiographic position, San Cristián is unique in that the site is adjacent to a steep hillside, which may have contributed considerable run-in. San Cristián's location in the eastern foothills of the central highlands may also have contributed to the anomalously high soil water recharge recorded there (Table 2; Fig. 3), which possibly resulted from increased precipitation by orographic uplift.

Gravimetric water content was measured as in Gardner (1986) in soil samples obtained from the 0·10, 10·30, 30·50 and 50·100 cm depth layers by using an 8-cm hand auger in spaces between *L. tridentata* shrubs along the same transects established for the plant water

Table 2. *Seasonal water recharge (positive values) and depletion (negative values) (mm) in the upper meter of soil from December 1986 to April 1989 at six study sites in the Central Desert of Baja California, Mexico*

		Study sites											
Season	Year	El Progreso		Cataviña		Laguna Chapala		El Crucero		San Cristián		Los Frailes	
Winter	1987	44	−2	25	−22	50	−46	17	−42	46	−81	21	−24
Spring		0	−20	0	−21	0	−27	12	−13	20	−30	0	−17
Summer		0	−48	5	−1	23	−0	4	−33	30	−21	0	−4
Fall		63	−0	9	−8	57	−7	23	−0	82	−20	31	−0
Winter	1988	29	−33	58	−40	nd*	nd	35	−27	13	−40	0	−20
Spring		0	−40	0	−22	nd	−66	0	−18	0	−20	0	−7
Summer		12	−10	1	−3	13	−12	19	−11	0	−75	9	−5
Fall		14	−17	15	−4	0	−5	27	−17	183	−0	56	−5
Winter	1989	40	−32	13	−18	71	−60	11	−40	0	−134	0	−49
Subtotals		202	−202	126	−139	214	−223	148	−201	374	−421	117	−131
Initial-final water content		1		14		10		52		47		15	
Totals		203	−202	141	−139	224	−223	200	−201	421	−421	132	−131

The values represent the sum of changes in average water content ($n = 3$) recharge and depletion during the seasons (winter = January, February, March; spring = April, May, June; summer = July, August September; fall = October, November, December).

* nd = not determined.

potential measurements. Representative samples of moist whole soil (500 g) were weighed fresh in the field on (tared) sheets of aluminum foil to an accuracy of 1 g by using a triple-beam balance (calibrated and protected from wind). The soil samples, wrapped in aluminum foil, were then placed in paper bags and transported to the laboratory, where they were weighed again after drying at 100–110°C in a forced-draft oven for at least 24 h. Rocks were frequently encountered during augering, but samples were considered acceptable if the bore hole reached at least the 75 cm depth. Auger holes were filled back to minimize alterations of the soil matrix in the sampling transects.

For each sampling, the water content in the 0–100 cm soil layer (= soil water storage), was calculated by summing the depth-equivalent (e.g. mm/unit area) water contents of the 0–10, 10–30, 30–50, and 50–100 cm soil layers. The depth-equivalent water content was calculated by multiplying the gravimetric water content by the bulk density of the soil and the depth increment of each soil layer, as described in Gardner (1986). Recharge of the soil water reservoir was defined as increases in water content, due to infiltration, in the 0–100 cm soil layer; and depletion as decreases, due to evapotranspiration and deep drainage. Evapotranspiration was estimated as in Hillel & Tadmor (1962) and Branson *et al.* (1976) as the difference (adjusted for recharge and considering drainage as negligible) between maximum and minimum soil water storage. No attempt was made to measure deep drainage or run-off/run-in relationships.

Soil water potentials were estimated from water retention curves determined as in Klute (1986) and Rawlins & Campbell (1986) by using a thermocouple psychrometer (NT-3 nanovoltmeter thermometer, Decagon Devices, Pullman, WA) and repacked soil samples from each site and for each depth increment. The water retention curves were used to estimate available water (Table 3).

Bulk density of the soil was measured at each site by using the auger holes used for sampling soils for water content. The void volume of the holes was measured as in Blake & Hartge (1986) (except that measurements were made by volume instead of mass) by filling the holes with measured volumes of (compacted) dry, sieved (2 mm) river sand. The difference in volume between compacted and loose sand was determined by filling 1 L plastic graduated cylinders ($n = 5$) with loose sand and then compacting to constant volume by smartly tapping the cylinder on the ground several times. The void volume of the hole was then calculated as the volume of loose sand required to fill it. Soil quantitatively removed from the bore holes was dried for several days at 100–110°C (soil samples used for moisture determinations were added back) and weighed.

Pits were excavated near the transects used for plant sampling, and soils were described and classified in the field (Table 1) as in Soil Survey Staff (1975). Samples taken from soil horizons in the pit faces were air-dried and passed through a 2 mm sieve. Saturated pastes were prepared with deionized water, and soil solution was extracted as in Rhoades (1982). The pH of the saturated pastes and the electrical conductivity of the saturation extracts (EC_e) were measured by using a model 4503 Selectro-Mark Analyzer (Markson Science, Phoenix, Arizona). Soil texture was determined by using a hydrometer as in Gee & Bauder (1986).

Results

Plant cover was lowest at Los Frailes, but was significantly higher at all other sites except El Progreso (Table 1). Richness of perennial species was also lowest at Los Frailes (12), but ranged from 18–32 at the other five sites. All sites, except San Cristián, have recent soils with little horizon development (Entisols) which can be classified as either sandy (Psamments) or loamy (Orthents) (Soil Survey Staff, 1975). The soils at Cataviña, El Crucero, and Los Frailes are deep, structureless sands. The soil at San Cristián, an Aridisol, showed strong horizon development, and may meet the criteria for a subsurface

Table 3. *Estimated components of the soil water budget and water retention characteristics of the soil at study sites in the Central Desert of Baja California, Mexico*

Study sites	Mean annual precipitation* (mm)	Total recharge as per cent of precipitation at El Progreso	Estimated annual evapotranspiration†	Total porosity‡ (0–1 m)	Field capacity§ (−0·03 MPa)	Wilting point§ (−1·5 MPa)	Sparingly available§ (−10·0MPa)
			(mm)				
El Progreso	132 ± 31	76	76 ± 8	458	263	137	76
Cataviña	115‖	47	43 ± 19	397	160	16	1††
L. Chapala	110 ± 50¶	80	77 ± 3	460	215	43	21
El Crucero	110 ± 67**	56	61 ± 25	405	250	27	8††
San Cristián	n.a.	—‡‡	150 ± 29	459	271	143	65
Los Frailes	n.a.	44	46 ± 14	386	187	16	0††

* Mean ± S.D. (n = 2: Jan–Dec '87, '88). Total precipitation December 1986–May 1989; El Progreso, 266; L. Chapala, 233; El Crucero, 233.

† Mean ± S.D. (n = 3). Calculated by subtracting minimum water storage from (maximum water storage + additional recharge) for each recharge-depletion cycle. Minimum water storage values for 1988 were used for 1989 calculations.

‡ Estimated by assuming particle density of 2·65 Mg m^{-3}, and measured bulk densities: El Progreso = 1·44; Cataviña = 1·60; L. Chapala = 1·43; El Crucero = 1·58; San Cristián = 1·43; Los Frailes = 1·63 Mg m^{-3}.

§ Estimated from water retention curves determined by thermocouple psychrometry (unpublished data).

‖ Clark *et al.*, 1993.

¶ Records incomplete.

** Recorded at Punta Prieta, ~40 km SE (records incomplete).

†† Extrapolated value.

‡‡ Results in value >100% (141%).

n.a. = not available.

horizon enriched with leached clay (argillic horizon). At all sites, surface soils were near-neutral in pH and non-saline (Table 1).

Soil water regime

Annual precipitation during the study period was near the long-term mean (Fig. 2, Table 3). According to the classification of Schonher & Nicholson (1989), the El Niño event of 1986–7 was of the 'dry' type, and it was followed by a strong La Niña event during 1988–9 (R. A. Minnich, pers. comm.). Three periods of significant soil water recharge were registered at all six sites; these occurred during the fall and winter of 1986–7, 1987–8, and 1988–9 (Fig. 3). Winter 1986–7 was characterized by a number of small frontal storms. In winter 1987–8, the majority of precipitation fell during two major frontal events in December and January. The northern sites were relatively dry during late fall and early winter 1988–9, but two strong soil recharge events (probably from precipitation of tropical origin) were registered at the southern sites. During the study period, recharge in response to spring precipitation was rare, but common in summer and autumn (Fig. 3, Table 2). If the four sites on the Pacific side of the divide are considered together, recharge during summer and fall averaged 40% of the total, but it averaged 80% of the total at the two sites on the Gulf of California side (Table 2).

Because of differences in the retention of water by soils of different textures, sandy soils (Cataviña, El Crucero, and Los Frailes) and loamy soils (El Progreso, Laguna Chapala, and San Cristián) were grouped together for comparison. The patterns of soil water recharge and depletion for the sites on sandy soils were similar. In the sandy soils, cumulative recharge ranged between 120–150mm, and depletion between 130–200 mm (Table 2). In the loamy soils, cumulative recharge ranged between 200–375 mm, and depletion between 200–425 mm. Depletion of moisture from the soil profile was much faster in the sandy than in the loamy soils.

Comparisons of water storage in the loamy- and sandy-soil sites by one-way analysis of variance revealed significant differences ($p \leq 0{\cdot}05$) between all sites except Cataviña and Los Frailes (Fig. 3). The water regimes at El Progreso and Laguna Chapala differed significantly much of the time, but soil water storage at San Cristián was greater than at the other loamy soil sites almost all the time. This was likely because that site received both more precipitation and run-in than the other sites. On the other hand, analysis of variance (not shown) revealed that changes in soil water content (i.e. recharge and depletion) did not differ significantly between sites. This indicates that, although there were significant differences in the amounts of water held in the soil (except at Cataviña and Los Frailes), the magnitudes of soil water recharge and depletion through time were roughly similar (but highly variable) at all sites, regardless of soil type. Estimated evapotranspiration was lowest in the sandy soils, intermediate for sandy loams and highest for San Cristián (Table 3).

Leaf water potential

The time pattern of leaf water potential was similar to that of water storage in the soils: maximum during periods of recharge and decreasing during depletion (Fig. 3). Analysis of variance (not shown) revealed no significant differences in leaf water potential between sites. Predawn leaf water potential in *L. tridentata* was moderately correlated with soil water content at individual sites regardless of soil type (Table 4). When sites having similar soil texture were considered together, this relationship was weaker in the loamy than in the sandy soils. A logarithmic fit explained the variability in the data slightly better than a linear relationship (Fig. 4). In the two woody shrubs (*L. tridentata* and *S. chinensis*), the relationships between midday leaf water potential and soil water content were weaker and

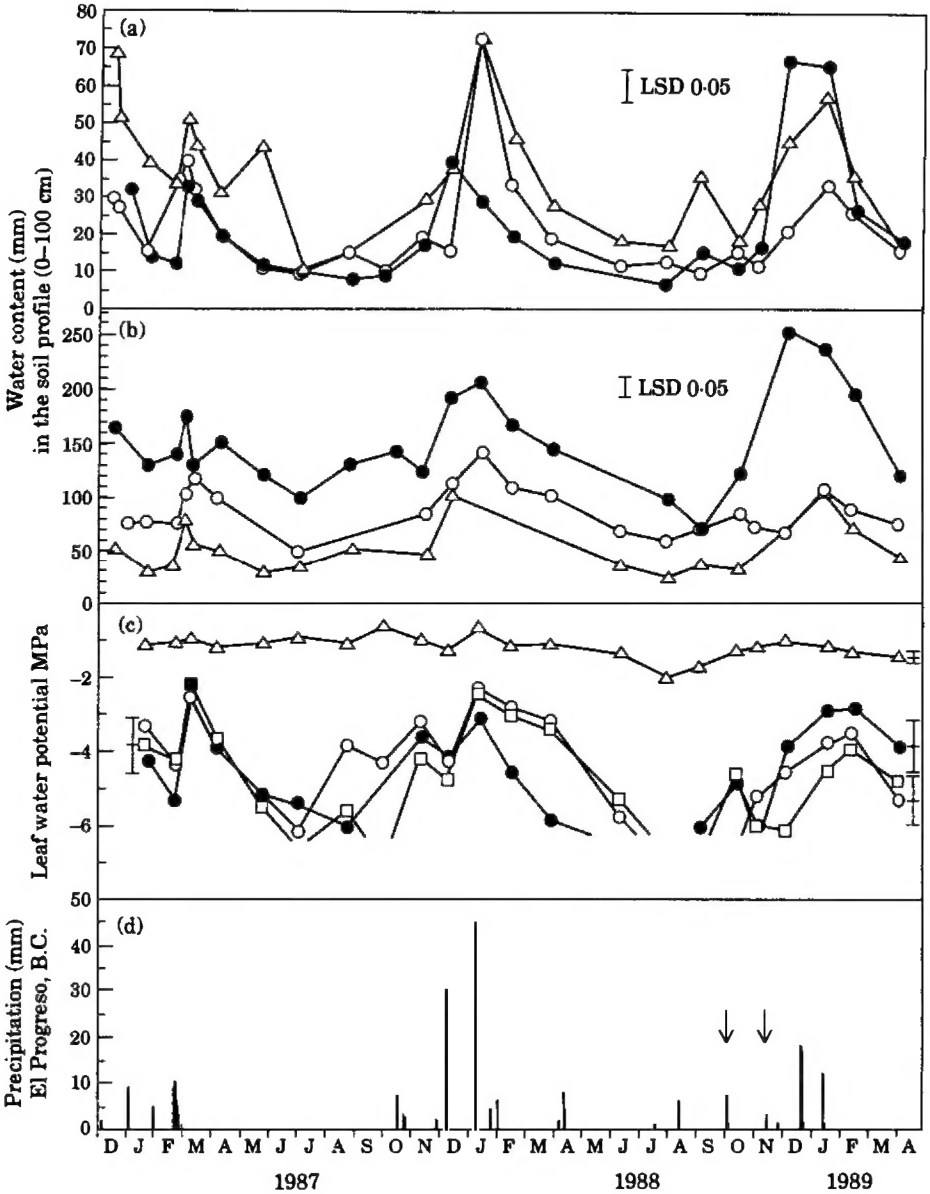

Figure 3. Time courses of soil water storage at sandy (a) and loamy soil sites (b), leaf water potential at two sandy soil sites (c), and precipitation at El Progreso (d), the only site for which data are reliable and complete. For soil water storage, the values represent the average ($n = 3$) of the sum of (depth-equivalent) gravimetric water content in the 0–10, 10–30, 30–50, and 50–100 cm soil layers. Water storage was compared between sites by using one-way analysis of variance. The bars represent the minimum difference between two means required for significance at the 5% level. For leaf water potential, the values represent the mean ($n = 3$) of predawn measurements in twigs of *Larrea tridentata*, *Simmondsia chinensis* and *Fouquieria columnaris* obtained with a pressure chamber in which the pressure relief valve activated at ~6·5 MPa. Leaf water potential in *L. tridentata* was compared between Los Frailes and Cataviña by one-way analysis of variance; no significant difference was found. The error bars are ±1 standard error of the treatment, where each species represents a treatment. Daily precipitation was recorded in a bulk rain gauge operated by SARH at El Progreso, which is ~1 km S of the study site. The arrows indicate fall storms that produced little precipitation at El Progreso, but resulted in considerable recharge at the southern and eastern sites. (a) —○— = Cataviña; —△— = El Crucero; —●— = Los Frailes. (b) ---○— = El Progreso; —△— = Laguna Chapala; —●— = San Cristian. (c) —●— = *Larrea* (Los Frailes); —○— = *Larrea (Cataviña)*; —□— = *Simmondsia* (Cataviña); —△— = *Fouquieria* (Cataviña).

Table 4. *Matrix of simple correlation coefficients for the relationships between total soil water content* in the 0–100 cm layer and leaf water potential† of three perennial species at the six study sites in the Central Desert*

Sites	*Larrea tridentata*			*Simmondsia chinensis*			*Fouquieria columnaris*		
	Predawn	Midday	Difference‡	Predawn	Midday	Difference‡	Predawn	Midday	Difference‡
El Progreso	−0·66[c]	−0·55[c]	+0·22	−0·55[a]	−0·60[b]	−0·39	−0·50[a]	+0·02	+0·33
Cataviña	−0·69[c]	−0·75[c]	+0·26	−0·71[c]	−0·76[c]	+0·30	−0·47[a]	+0·26	+0·60[b]
L. Chapala	−0·70[b]	−0·72[b]	+0·36	−0·58[a]	−0·65[a]	+0·05	−0·52[a]	+0·03	+0·23
El Crucero	−0·64[b]	−0·64[b]	+0·09	−0·66[b]	−0·42	+0·33	−0·69[c]	+0·07	+0·56[a]
San Cristián	−0·70[b]	−0·47	+0·29	−0·66[b]	−0·57[a]	−0·18	Does not occur at site		
Los Frailes	−0·70[c]	−0·49[a]	+0·42	Does not occur at site			Does not occur at site		
Sandy soils§	−0·59[c]	−0·55[c]	+0·22	−0·57[c]	−0·52[c]	+0·25[c]	−0·49[c]	+0·26	+0·59[c]
Sandy loam soils‖	−0·51[c]	−0·43[c]	+0·31[a]	−0·28[a]	−0·27	−0·14	−0·14	+0·16	+0·17

* Sum of (depth-equivalent) gravimetric water contents (mm) in the 0–10, 10–30, 30–50, and 50–100 cm layers.
† Measured by using a pressure chamber (pressure relief valve released at ~65 bars).
‡ (Midday–Predawn), a few values ≤ 0 were not considered.
§ Cataviña, El Crucero and Los Frailes.
‖ El Progreso, Laguna Chapala and San Cristián.
[a b c], $p \leq 0{\cdot}05, 0{\cdot}01, 0{\cdot}001$, respectively.

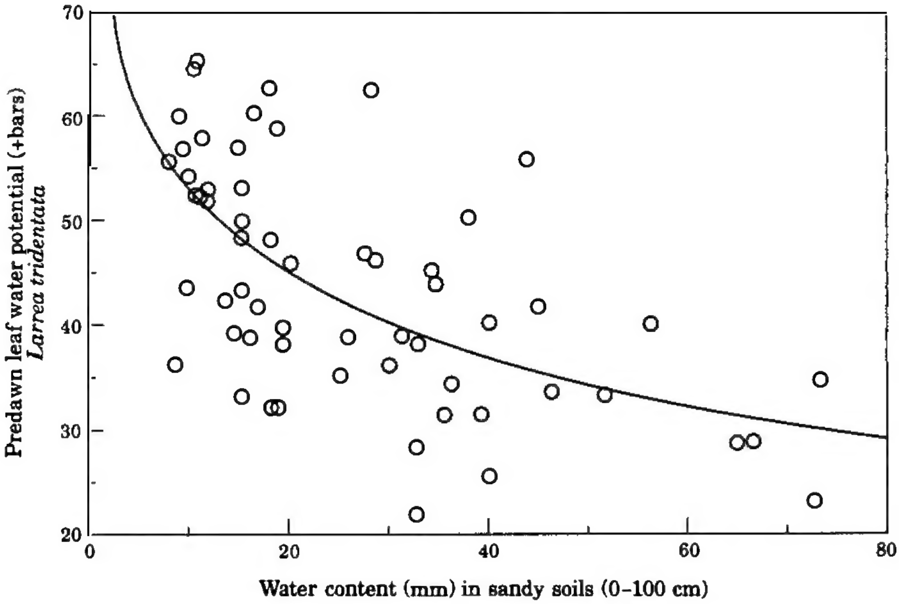

Figure 4. Relationship between average water content in the upper metre of soil ($n = 3$) at all three sandy soil sites (Cataviña, El Crucero, and Los Frailes) and average predawn leaf water potential ($n = 3$) in *Larrea tridentata* sampled at roughly monthly intervals during the study period. Leaf water potentials $< -6{\cdot}5$ MPa could not be measured and thus could not be considered. $y = -26{\cdot}23 \text{ Log}(x) + 79{\cdot}03$; $p \leq 0{\cdot}001$; $R^2 = 0{\cdot}39$.

more variable than those for the predawn measurement. The midday relationship was meaningless in the C_3 stem succulent *F. columnaris*. In the shrubs, the difference between midday and predawn leaf water potentials, which is probably governed by stomatal control on transpiration, was only weakly related to soil water content. But midday – predawn potentials were moderately correlated in the stem succulent *F. columnaris* in the two sandy-soil sites where it occurred.

Discussion

Water regimes

The patterns of water regimes in the present work were most similar to those reported for principal habitats of the Negev Desert (Hillel & Tadmor, 1962), except that recharge during summer and early fall is apparently rare near the eastern Mediterranean Sea. Soil water recharge during the study period occurred mostly as a result of late fall and winter rains (Fig. 3), with a few recharge events during summer and early fall. It has been hypothesized that *F. columnaris* (and perhaps other plants native to the Central Desert) requires the stimulation of summer rainfall for establishment and survival (Humphrey, 1974). A significant decrease in leaf water potential occurred in *F. columnaris* in response to rains during July and August 1988 (Fig. 3), and may indicate a period of active transpiration; this species generally flowers in those months (Humphrey, 1974; Wiggins, 1980). Recharge amounts during late summer and early fall, while not large, appeared to be sufficient to improve the establishment and water economy of desert plants.

The amounts of water stored in soils, as well as estimated evapotranspiration (depletion) were similar to those in water regimes of other arid regions (Shreve, 1934; Hillel &

Tadmor, 1962; Winkworth, 1970; Branson *et al.*, 1976; Sammis & Gay, 1979, Schlesinger *et al.*, 1987). Results presented here are consistent with those previous studies in that water storage ranged between 10–70 mm for sandy soils, and between 50–150 mm for the loamy-soil sites of El Progreso and Laguna Chapala (Fig. 3).

Estimated annual evapotranspiration in the present work was 45–60 mm in sandy soils, ~75 mm in loams at El Progreso and Laguna Chapala, and 150 mm at San Cristián (Table 3). The anomalously high annual recharge and depletion at San Cristián (100–250 mm) can be explained by (i) higher precipitation than at the other sites during the study period, (ii) run-in from a steep nearby slope, and (iii) higher water retention by the finer-textured soil (Table 1). Although the explanation probably involves all three factors, water recharge at San Cristián in thefall of 1988 was greater than at other sites, and recharge during fall 1988 and winter 1989 was significantly higher at the eastern and southern sites (Los Frailes, San Cristián and El Crucero) than on the northern sites (Fig. 3). Therefore, this anomaly may have resulted from unusually high precipitation in the vicinity of San Cristián during the period of study. The loss of precipitation data for all study sites except El Progreso precludes clarification.

Soil water recharge at El Progreso and Laguna Chapala accounted for ~80% of precipitation, and was approximately equal to estimated evapotranspiration in these soils (Table 3). This is consistent with the results of Hillel & Tadmor (1962), who estimated that water depletion in rocky slopes and loessial plains in the Negev Desert was ~80% by evapotranspiration, 15–20% by run-off and 0–5% by deep drainage. However, in the sandy soils recharge accounted for only about half the precipitation. Because infiltration and percolation rates in sands are usually high (Hillel & Tadmor, 1962), much of the difference may be assigned to losses by deep drainage (run-off was probably negligible). In the finer textured soils, the presence of indurated petrocalcic horizons make losses by deep drainage unlikely (Graham & Franco-Vizcaíno, 1992).

Depletion of water in the soil profile to very low levels (< -10 MPa) has been observed in previous studies in dry regions (Winkworth, 1970; Branson *et al.*, 1976). Estimated minimum matric potentials were ≥ -10 MPa during spring and summer at all sites except El Progreso (Fig. 3; Table 3). Water content during dry periods in 1987 and 1988 was considerably below the -10 MPa content (76 mm) at that site.

Significant differences in water storage between sites occurred at specific times; this demonstrates the variability of precipitation in time and space (Fig. 3). Comparison of water storage at Cataviña and Los Frailes, which are nearly on opposite ends of the gradient, but on similar soils derived from quartz diorite, revealed no significant differences in water storage during the period of study (Fig. 3; Tables 2,3). However, perennial plant cover was significantly higher at Cataviña than at Los Frailes (Table 1), and long-term precipitation data indicate that the Gulf coast is drier than the central highlands (Fig. 2). Across this gradient, the availability of water may be additionally reduced by a combination of (i) a higher proportion of rainfall occurring during summer (when vapour pressure deficits are much higher), (ii) longer drought and more variable precipitation, and (iii) much lower moisture inputs from fog (for which data are not available). Soil water recharge did not occur at Los Frailes in five of the nine seasons studied, but at Cataviña there was no recharge in only two of the nine seasons (Table 2). Thus, during the period of study, longer drought at Los Frailes was important in reducing the reliability of moisture. Longer and more frequent droughts may mostly explain the low plant cover and species richness in this habitat, and thus the differences between the major plant communities described by Wiggins (1980).

Leaf water potential and soil water content

The weak to moderate relationships between soil water content and leaf water potential in *Larrea*, *Simmondsia*, and *Fouquieria* at specific sites in the Central Desert (Table 4) were in

the same range as those reported by Branson *et al.* (1976) [r = 0·55–0·9] for several species of desert shrubs in Colorado. They used a pressure chamber capable of measuring leaf water potentials < -10 MPa, and the higher correlation coefficients they reported may have been due to the stronger relationship obtained when soil water contents are low. During periods of ample soil water supply, the influence of environmental factors other than water content on leaf water potential may be stronger (Branson *et al.*, 1976). Results presented here (Figs 3,4; Table 3) are consistent with those of Schlesinger *et al.* (1987), who reported measurable decreases in soil water potential below $-6{\cdot}0$ MPa.

The moderate relationship between soil water content and the difference between midday and predawn water potentials in *F. columnaris* in sandy soils (Table 4) indicates that soil water supply exerts strong control on stomatal opening in the C_3 stem succulent. In the non-succulent ephemeral leaves of *F. columnaris*, short-term drought resulted in decreased leaf conductance and small diurnal fluctuations in leaf water potential (Franco-Vizcaíno *et al.*, 1990). However, when soil moisture was abundant, active daytime transpiration caused strong diurnal fluctuations (-1 to -2 MPa) in leaf water potential, with minima at midday. Gas exchange was not observed across the green bark, and stem photosynthesis apparently serves to recycle endogenous respiratory CO_2 to maintain energy reserves for rapid production of leaves after rain. Results presented here indicate that *F. columnaris* maintains relatively high water potentials (Fig. 3), probably by uncoupling its water-storing tissues from the soil and atmosphere during drought.

Leaf water potential measurements may be an easy and inexpensive way to monitor seasonal soil water recharge and estimate regional forage production (Branson *et al.*, 1976). Predawn leaf water potentials in *L. tridentata* growing in coarse-textured soils may be a useful indicator of soil water status (Fig. 4). However, stronger relationships may be obtained by using a pressure chamber capable of measuring leaf water potentials $< -6{\cdot}5$ MPa. Much of the variability in the data presented in Fig. 4 probably resulted from the random timing of sampling; this same difficulty will be faced in any attempt to characterize regional soil water recharge in a remote region.

Summary

The time pattern of soil water storage was similar in soils of similar texture; water contents were higher, and water depletion was slower on the loamy than on the sandy soils. In soils of similar texture, significant differences in water storage largely reflected the variability in time and space of recharge events. During the study period, increased aridity in two sandy soils located near the ends of the gradient studied was expressed not as significantly smaller amounts of water recharge in soils, but as longer periods of drought. In loamy soils, water recharge in the surface one-metre soil layers accounted for ~80% of the precipitation, and was approximately equal to estimated evapotranspiration; the remaining 20% probably ran off. In the sandy soils, recharge accounted for only 50% of precipitation; and it is likely that at least 30% of precipitation drained deeper than one metre. At the six sites studied, moderate relationships were found between soil water content and predawn leaf water potential in *Larrea tridentata*. This relationship was slightly weaker when sites of similar soil texture were grouped together for comparison. Leaf water potential in indicator shrubs, when calibrated with soil water content in soils of different textural classes, may be a useful index for monitoring water regimes in remote regions where infrastructure is scarce.

This study was part of the French-Mexican project 'Terrestrial Ecology of Baja California Norte' and was supported by a grant (PCECCNA/041722) from the Mexican National Council on Science and Technology (CONACyT). Arturo Arroyo Dominguez, Agustín Ledesma Arellano, Mireya Balcázar Luna, Eric Molina Becerril, and Mario Salazár Ceseña helped with field and laboratory work. Plant cover data were provided by Alain Walkowiak Bravo. Martín Escoto Rodriguez determined the water retention characteristics of soils.

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